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Opinion

# Leveraging Motivations, Personality, and Sensory Cues for Vertebrate Pest Management

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**Managing vertebrate pests is a global conservation challenge given their undesirable socio-ecological impacts. Pest management often focuses on the 'average' individual, neglecting individual-level behavioural variation ('personalities') and differences in life histories. These differences affect pest impacts and modify attraction to, or avoidance of, sensory cues. Strategies targeting the average individual may fail to mitigate damage by 'rogues' (individuals causing disproportionate impact) or to target 'recalcitrants' (individuals avoiding standard control measures). Effective management leverages animal behaviours that relate primarily to four core motivations: feeding, fleeing, fighting, and fornication. Management success could be greatly increased by identifying and exploiting individual variation in motivations. We provide explicit suggestions for cue-based tools to manipulate these four motivators, thereby improving pest management outcomes.**

## Highlights

The explicit consideration of individual traits is central to enhancing effective vertebrate pest management.

We provide a heuristic framework for understanding animal motivations and cues across spatial scales.

Focussing on individual motivations can improve population-level control measures and reduce the impacts of problematic individuals that cause the most damage.

Incorporating principles of behavioural ecology will increase the effectiveness of any intervention while providing an opportunity to test behavioural theory in a natural context.

## Looking Beyond the 'Average' Individual in Vertebrate Pest Management

Vertebrate pests, including invasive or overabundant predators and herbivores, frequently come into conflict with economic, social, and biodiversity values. Mammalian predators are responsible for some of the most devastating losses to native biodiversity [1] and frequently harm humans, their livestock, and pets, while herbivores can cause agricultural damage, vehicle collisions, and ecosystem-level impacts including overbrowsing [2,3]. Mitigating the impacts of vertebrate pests thus presents one of the major challenges currently facing wildlife managers. Managers require effective strategies to: (i) reduce pest populations (e.g., by attracting individuals to traps or toxic baits), and (ii) deter individuals from sensitive areas or valuable species (e.g., threatened prey or plant species, livestock, agricultural, and forestry sites). Yet, pest control measures are often only partially effective [4,5], with some individuals avoiding lethal control or ignoring deterrents. Attractants and deterrents typically target the 'average' individual in a population, with the goal of maximising the number of animals responding to stimuli. However, the most intractable challenges of vertebrate pest management may occur precisely because some individuals do not behave like the average, and therefore, are not effectively targeted.

Within a pest population, individuals exhibit a range of responses to management actions. Deviations from the average response may be transient (e.g., dependent on internal state, body condition, current perceived risk, or density of conspecifics) [6], or may represent persistent, individual-level behavioural differences ('personalities') [7,8]. By understanding the drivers of individual-level differences in behaviour, management can be optimized to target not just the average individual, but the full range of behavioural types within a population. Such insights may be particularly valuable in managing **rogue** and **recalcitrant** individuals (see Glossary), two non-exclusive behavioural types that occur in many pest populations and often have

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disproportionate economic and conservation impacts. Rogues (also known as ‘problem individuals’) cause inordinate damage [3,9], often due to low responsiveness to deterrents aimed at excluding or deflecting them from valued species or areas. Recalcitrants are particularly difficult to attract to **management devices.** Their survival allows populations to re-establish quickly after the majority of the pest population has been removed, and, in the case of invasive predators, recalcitrants can maintain predation pressure on native species [10]. Anticipating and targeting the full range of behavioural variation within a pest population could substantially enhance the effectiveness of control efforts and reduce the risk of inadvertently favouring management-resistant behavioural types [8,11].

Here we present a framework to explicitly incorporate individual behavioural variability into vertebrate pest management. This framework is based on the fact that, like all behavioural decision-making, an individual’s decision to move towards an attractant or avoid a deterrent is largely driven by a set of fitness-based motivations characterized by **the 4Fs** of animal behaviour [12]: feeding (energy demands), fleeing (predator avoidance), fighting (competition), and fornicating (mating). While behaviour can be governed by other specific **cues**, the underlying motivations ultimately involve these 4Fs (e.g., attraction to conspecifics usually reflects feeding, safety, agonistic, or mating needs). We explore how differences in these motivations underlie individual-level differences in pest responses to management actions, and how these motivations can be exploited to increase the effectiveness of attractants and deterrents. We build on previous work (e.g., [3,8,9]) by providing recommendations for enhancing management effectiveness across all pest behavioural types involving manipulation of exposure to sensory cues (Box 1).

### Box 1. A Behavioural Framework for Pest Attraction and Deterrence

Effective pest management often depends on animals being motivated to interact with a management action. Sometimes the goal is attraction (e.g., attraction to traps, monitoring devices, or less sensitive areas), and sometimes deterrence (e.g., deterring pests from valuable resources or vulnerable species). We present a simple heuristic model that provides a framework for understanding the various motivators acting on an animal’s decision to approach and interact with a management device or avoid a sensitive area. Our model is based on Brown’s classic equation describing patch-quitting decisions while foraging under the risk of predation [66].

We consider that the probability, *P*, of interacting with a stimulus (e.g., a trap, bait station, or other resource like a crop or threatened prey species), once it is detected, is shaped by three motivational elements: (i) the value of the attractive stimulus (*VA*, be it a food cue, a social cue, or other information), (ii) the perceived danger (*PD*) of interaction, and (iii) the missed opportunity costs (*MOC*) (other food or mating opportunities the animal misses out on by interacting).

*P is proportional to VA–PD–MOC*

A wildlife manager wishing to change interaction probability has three ‘levers’ to pull: the attractiveness of the stimulus, the perceived danger of the stimulus, or the animal’s perception of missed opportunity costs. Adjusting any one of these levers changes the probability the animal will interact with the stimulus.

Wildlife managers intuitively tinker with these elements when trying to manage pest species, but we argue that practitioners have overlooked the role of an animal’s state and traits (i.e., its personality, experience, physiology, and reproductive condition) in shaping its motivations and responses.

Attempts to increase rates of interaction with devices have largely tried to increase *VA* by creating better food-based attractants in the search for a so-called super lure [24]. However, food-based lures are less effective when there is abundant alternative food available (higher *MOC*) or the device is perceived to be too risky or threatening (higher *PD*). There is also a large body of work attempting to decrease the interactions of animals with important assets (such as seedlings or crops) by increasing *PD* at the site through the use of predator cues [57]. These attempts routinely fail if the assets are too valuable for animals to ignore (high *VA*), too easy to find relative to other foraging opportunities (low *MOC*), or if the animals habituate in the absence of real risk [67].

## Sensory Cues

Animal decision making depends on sensory cues (sight, sound, smell) that convey information about resources [13,14], predation risk [15,16], heterospecifics [17], or conspecifics [18]. Cues provide the link between a pest management objective (attract or deter) and the behavioural responses of the targeted animals (Figure 1). Here, we review the types of sensory cues and how they can be utilized in a management context. We then draw on signal detection theory (SDT) for insights into maximizing cue effectiveness based on the range of motivations, states, and perceptual abilities in a pest population.

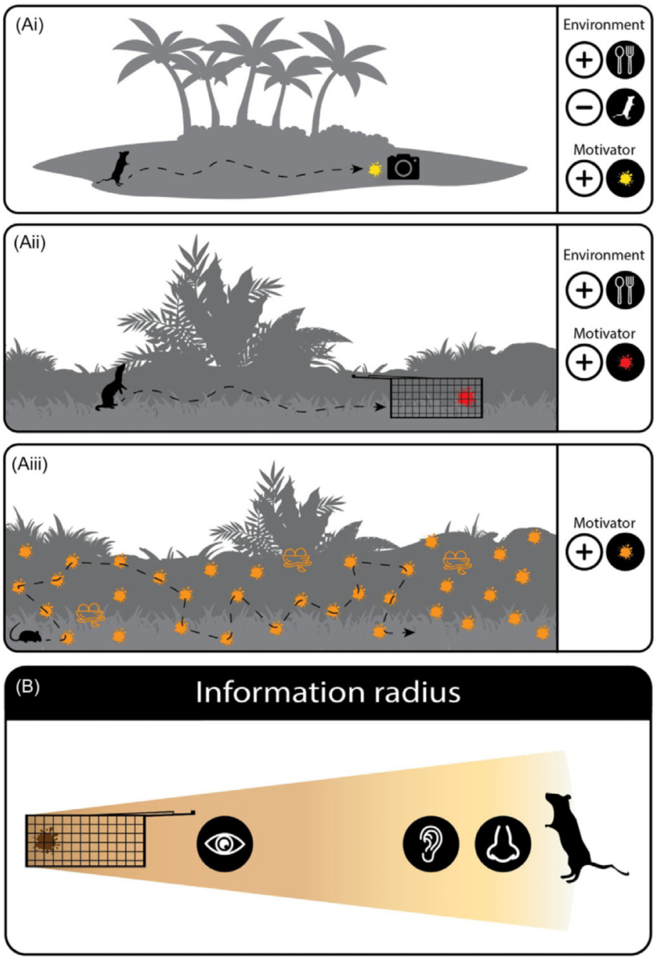


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Figure 1. Novel Approaches that Manipulate Animal Motivations for Pest Management. (A) (i) A novel sex motivator (yellow dot) to increase detection of pest animals (such as rats, shown here) at low densities. For example, in an island invasion scenario with low pest animal density but high food availability, a social cue, such as a female pheromone, is predicted to have high attractant value (*VA*). (ii) A sympatric predator or competitor cue (red dot) to increase trap success. For example, when food availability is high, a predator odour that conveys information on enemies can have high *VA* (see Box 3). (iii) A novel use of food odour to reduce motivation to pursue a particular food type. For example, the odour of the target food such as bird eggs (orange dots represent nest odour) is distributed prior to or during the breeding season to reduce the value of this stimulus (*VA* of prey cue) and therefore the probability (*P*) that a predator will interact with the threatened prey species. (B) Sensory cues provide information over different spatial scales and influence decision making as an animal moves towards an introduced stimulus. While the detectable range and perceived information content of a given cue type can vary, acoustic, olfactory, and visual cues each operate over characteristic spatial scales, and can convey multiple types of information. Sound and scent cues operate over larger scales, while visual cues are likely to become more important when the animal is close to the stimuli, depending on the dominant sensory modalities of the target species.

## Glossary

**Animal personality:** the phenomenon whereby individuals of the same species differ systematically in their behavioural tendencies. These differences are consistent over time and often correlated across different situations and contexts.

**Cues and cue reliability:** cues are sensory features of a situation that can be used to evaluate its expected value. A cue is reliable if it provides accurate information about the situation's value.

**Management device:** wildlife monitoring or control tools, or deterrents used to detect, remove, or deter pests from species or areas. Examples of management devices include monitoring tools (e.g., trail cameras, tracking tunnels, hair snares, funnel traps), lethal-control traps (e.g., Victor trap, conibear trap), live-capture traps (e.g., cage trap, foothold trap, Sherman trap, Larsen trap), and frightening devices (e.g., Hawk Kites, fladry, bioacoustics).

**Rogue:** an individual that causes disproportionately high levels of damage.

**Recalcitrant:** an individual that avoids standard control measures.

**The 4Fs:** the four main factors that motivate behavioural decisions: feeding, fleeing, fighting, and fornication.

An animal's decision to engage with a sensory stimulus can be divided into two stages: encounter and response. An encounter (i.e., cue detection) depends on the animal's perceptual abilities [19] as well as the spatial range of the cue type(s) used (see below). Once encountered, the probability that an animal responds to a cue (i.e., approaches and interacts or moves away) depends on the animal's state (i.e., the relative importance of each of the 4F motivators) and its assessment of the environmental context in which the cue is embedded (e.g., missed opportunity costs, see Box 1) [18].

Managers can take advantage of the information offered by sensory cues, and the spatial scales over which they operate (Figure 1B) to exploit multiple behavioural motivators, ideally together (Figure 1A). Acoustic cues operate over the largest spatial scales, drawing or repelling animals from beyond the immediate vicinity of the cue source. Acoustic cues signalling danger (e.g., from predators or humans) can deter target animals from relatively large areas [15,20] or reduce foraging impacts where lethal control is not possible or desirable (e.g., with native 'rogues') [21,22]. Alternatively, broadcasting vocalizations of prey or conspecifics can attract individuals over long distances [23].

Olfactory cues can also be effective over intermediate to large spatial scales and provide a range of information types. At high population densities, essential resources are limited, leading to strong conspecific competition. Olfactory cues that represent food, a mainstay of traditional pest management, may be highly effective in these situations. However, at lower population densities (e.g., following lethal control), food resources may not be limited and thus may not be a strong attractant. Olfactory social lures, such as conspecific or competitor scent, are then powerful alternatives to food lures, exploiting three of the four Fs that motivate behaviour (i.e., fighting, fear, and/or fornication) [24–26] (Figure 1A,i,ii). Olfactory cues that signal danger, such as predator odour [27] or territorial scent marks [28], can reduce the impacts of pests. Though examples are rare, applying odour cues can change pest behaviour, such as camouflaging native prey to reduce the impacts of invasive predators [29,30] (Figure 1A,iii).

Visual cues typically operate at the smallest spatial scales and have been used successfully to lure or deter pests**.** For example, a toy mouse is an effective attractant for feral cats [31], fladry impedes canid access to livestock [32], and scarecrows deter pests from crops [33]. Simultaneous deployment of multiple cues may prove most effective at eliciting responses from an entire pest population given the different scales over which cues operate, the diversity in individual responses, and the greater realism that multiple cues provide [34].

Importantly, whether a cue attracts or deters an animal depends not just on the cue itself, but also on properties of the individual and the environmental context. These include: (i) the animal's state, (ii) how its past experience shapes its assessment of risk and reward, (iii) how well cues can be discriminated from each other (cue uncertainty) and from 'noisy' background environments, and (iv) the relative costs of over- or under-responding to the cue [35]. SDT integrates the animal's assessment of cues and their reliability with the costs and benefits. This includes the costs of uncertainty and unavoidable errors. SDT provides a useful framework linking behavioural variation to the effectiveness of different management options (Box 2).

Given the importance of an animal's perceptions, learning from past experiences can play a critical role in determining an individual's response to a particular cue type [36]. For example, animals can become sensitive to cues associated with aversive experiences such as trapping and handling, Box 2. Signal Detection Theory

Signal detection theory (SDT) provides insights into how cues, past experiences, and cost-benefit asymmetries influence animal attraction to a device or avoidance of deterrents [36,68]. SDT typically simplifies situations into two types: good (food, safety) versus bad (risky). An animal has a prior assessment of good and bad based on experience. It uses a cue to adjust its assessment of the current situation and then responds, balancing the relative costs of two potential errors: the cost of being inappropriately attracted to a bad option versus the cost of unnecessarily avoiding a good one.

Animals are more likely to be trapped if the trap appears 'good'; for example, emanates cues associated with high attractant value (*VA*) and low perceived danger (*PD*). By contrast, they will be more difficult to trap if, in their past, situations resembling the trap were perceived as risky. The current environmental context also matters. Animals are more willing to enter a trap if they are very food-limited (since the cost of rejecting a trap baited with valuable food is high), and also more willing to enter a trap with moderate *PD* provided the outside environment appears even more dangerous.

SDT also emphasizes **cue reliability**; that is, not just whether the trap appears good or bad, but also how well the animal was previously able to use cues to distinguish good versus bad. If, over generations, certain cues have consistently and accurately indicated high- versus low-quality options, animals may have evolved to rely heavily on those cues. This is what makes some animals susceptible to evolutionary traps, when previously reliable cues lead them astray [69]. Alternatively, animals can learn about cue reliability from their experiences. If an animal evolved or developed in an environment where it could reliably determine whether trap-like situations were safe or dangerous, it should be willing to enter a trap that is designed to appear safe and attractive. By contrast, if the animal evolved or developed in an environment where it was difficult for it to use cues to distinguish safe versus dangerous situations (i.e., low cue reliability), then even if a trap appears safe and rewarding, the animal will likely ignore those cues. That is, 'recalcitrant' animals might be cautious not just because their environment is particularly dangerous, but because of the uncertainty of their cues. For these wary animals, it is important to give them numerous experiences with 'traps' that provide safety and food rewards (i.e., prebaiting) to train them to trust cues that later lure them into traps.

and become 'trap-shy', or conversely habituate rapidly to cues or objects that are perceived as inconsequential and ignore them [37]. Social learning can also lead to problematic behaviour [38]. For example, conspecific distress signals can teach rats to avoid traps [39], and maternal learning increases the likelihood that offspring of problematic grizzly bears *(Ursus arctos)* will also become rogues [40]. Learning can be used to target rogues and recalcitrants in different ways. For recalcitrants, managers should prioritise baits and devices perceived as appealing and safe. Wary individuals may consume sublethal doses or evade capture despite triggering a trap, and the negative experience will make the recalcitrant more intractable. Rogue animals need to be deterred, with no (or very few) opportunities to learn that deterrents are benign. For example, playing different predator sounds from changing locations may encourage rogues to be more responsive to perceived danger (*PD*) cues and less likely to habituate.

## Individual Variability

In order to understand the variation in current pest management outcomes [41–44], and to develop the next generation of effective strategies, we must understand and exploit individual-level behavioural variation within pest populations. Three layers of individual characteristics shape the relative importance of the 4Fs: the demographic traits of age, sex and reproductive status; the labile characteristics of body condition (health, hunger) and experience; and, behavioural trait variation, known as **animal personality**.

The concept of animal personality recognizes consistent behavioural differences among individuals beyond those explained by their demographic traits, and labile characteristics [7]. Personality spectrums, including boldness, exploration, activity, sociability, and aggressiveness, often co-vary in a behavioural syndrome; for example, a positive correlation between boldness and aggressiveness [45]. These traits shape how individuals perceive their environment and thus narrow their behavioural repertoires and responses. For example, boldness affects the foraging behaviour of individuals in response to predation risk [46,47]; exploration [48], and boldness [49] can affect home range size; exploration can affect capacity to solve food reward or escape problems [50]; activity-exploration can affect individual trapability [51]; and both sociability and aggressiveness affect attraction to, or avoidance of, conspecifics [52,53]. While personality differences are not the sole factor affecting responses to cues, personality types will likely respond differently to the same management strategy. Thus, using multiple motivators to target the range of personality types may substantially improve management outcomes.

The parallel literature on personality-dependent invasions into novel, human-altered habitats suggests that rogue individuals may be bold (exploiting habitats and resources others dare not visit), highly exploratory (exploiting resources others never find), or asocial (exploiting resources others never visit). Depending on social system, rogues may be dominant (leading others to exploit new resources), or subordinate (forced to use resources others do not). Conversely, recalcitrant individuals may be shy, cautious, asocial, or subordinate, avoiding risks associated with predation or with conspecifics [52,54]. Generally, focusing on the 'average' animal will inevitably fail to deliver reduced impacts. Instead, management strategies need to be adjusted to fit the goal (e.g., deterrence versus attraction) and the system. Different strategies can be tailored to fit different goals, and if a system has more than one type of problem individual (e.g., both rogues and recalcitrants), or even multiple pest species, then multiple strategies will be most effective.

If the goal is to deter rogues from sensitive areas or species, a key first step is to use available data (e.g., from failed strategies), natural history, or expert opinion to develop hypotheses on the behavioural tendencies of rogues in the specific context. If rogues are bold (and thus more responsive to rewards than risk), an appropriate management strategy could be to deter animals by providing alternative, high-quality food elsewhere [55], or even within the same food patch (as an attractant-decoy), as well as lowering the quality of the species (prey or plant) needing protection [56]. If, instead, problem animals are cautious (more sensitive to risk than reward), then they can be deflected by predator cues [27,57]; or if neophobic, by adding novel stimuli or inconspicuous devices [58].

Pest management programmes, by contrast, typically aim to attract all individuals to devices or baits. They may therefore benefit from using multiple sensory cues, or, given logistical constraints, multiple motivators for the same sensory cue, to ensure the range of behavioural types in a population is effectively targeted. If recalcitrants exhibit cautious behavioural types, they may be particularly responsive to manipulations of risk and safety than to other motivators such as food rewards. Novel cues can attract exploratory individuals, and conspecific or heterospecific cues can attract highly sociable or aggressive individuals.

## Management Applications

Rogues and recalcitrants are not only routinely problematic, but also require disproportionate responses to mitigate their impacts (Box 3). There are many ways to attract pests (high *VA*) to lethal or non-lethal devices using sight, smell, and sound cues that target the 4F motivations of animal behaviour. Examples include food lures, sound recordings of prey, scent glands of conspecifics, and predator body odour. Live animals are ideal because they include all three cues, although there are associated ethical considerations. Perceived danger can be reduced (low *PD*) by habituating animals to management devices before they are activated, for example, prefeeding with non-toxic baits, deactivating kill devices, or concealing devices with vegetation or soil. Missed opportunity costs can be minimised (low *MOC*) by deploying mostly food lures when competition for food is high; for example, when animal population density is high or food is seasonal; or by deploying mostly social lures (e.g., conspecific pheromones) when population density is low and animals are seeking mates.

### Box 3. Incorporating Animal Motivations Into Wildlife Management

Stoats (*Mustela erminea*, Figure I) are a problematic invasive predator that are trapped in New Zealand due to the damage they inflict on native birds [1]. As a small carnivore, stoats are vulnerable to predation by feral cats *Felis catus* and ferrets *Mustela furo,* the two largest invasive predators found in New Zealand. Stoats reduce the risk of antagonistic interactions by avoiding both predators, but, surprisingly, are attracted to the body odour of these same adversaries, suggesting that the information gained from odour inspection supersedes the potential risk of an encounter [16]. In experimental trials, ferret body odour stimulated the greatest attraction. Ferrets are closely related mustelids that rub sebaceous scent onto surfaces when caching food or establishing dens, both potential resources for stoats to exploit. Eavesdropping on sympatric predator scent has since been documented in other parts of the world (e.g., [70]), suggesting it is a common strategy for mesopredators to collect information and reduce risk.

To test whether predator scent increases monitoring accuracy (i.e., increased interactions), ferret body odour was deployed along with the standard attractive bait (rabbit meat) to create a natural, multicomponent cue that could be encountered at a kill or den site [26]. Stoat detections increased four-fold with the addition of predator odour, and estimated site occupancy changed from relatively rare (21%) to widespread (58%). Predator odour was then tested in a pest control context, where scent was added to every second trap at four established trapping operations created to protect kiwi *Apteryx* spp. and other endangered birds from stoat predation. For every ten stoats caught with the regular baiting approach, 25 were captured with added predator odour, an increase of 150%. Eavesdropping on predator cues was not limited to stoats: captures of weasels *Mustela nivalis* and detections of European hedgehogs *Erinaceus europaeus* also increased dramatically (+160% and +170%, respectively). Pest control had been in place for some time in this study, so pest numbers were low and presumably food availability was high. Therefore, recalcitrant stoats that had previously avoided traps with food lures may have been motivated to investigate traps with predator odour. Combining predator odour with a traditional food bait created a high-value source of information that increased the efficacy of management devices.


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Figure I. Stoat *(Mustela erminea)* Investigating predator (ferret *Mustela furo*) odour.

Vertebrate pest management may inadvertently select for particular traits in a targeted population, potentially resulting in recalcitrants that are difficult and expensive to manage. Maximising attraction with conspecific lures, deploying inconspicuous traps, and presenting control tools at the scale of the home ranges of shy individuals will help detect and control recalcitrants. SDT suggests recalcitrants will avoid risky, uncertain cues, so natural materials are preferable to metals or plastics to minimise the perceived danger associated with a device. Removal programmes alter the demographic structure and density of populations. Therefore targeting the 'average' individual overlooks density-dependent changes to behaviours and motivations as individuals are removed. Removing recalcitrants, which occurs towards the end of a removal programme at low densities, may require less emphasis on food lures and greater emphasis on 'safety cues' e.g., by placing devices in locations perceived to be safe.

An alternative strategy is to deter animals from valued resources by exploiting fighting and fleeing motivations using cues that signal danger (high *PD*). Historically, rogue animals have been specifically targeted by lethal control, an approach that often fails to achieve management objectives [9,43]. Rogues typically engage in high-risk, high-gain strategies, so deflecting animals away from valued resources may be a better approach. Repellents (e.g., alarming stimuli such as sirens or unpalatable compounds applied to plants) produce a localized and short-term effect, stopping behaviours already in progress. Conditioned food aversion can target rogue behaviour by manipulating the value of the prey (animal or plant). Livestock protection collars, with aversive olfactory or auditory cues, reduce bear and wolverine (*Gulo gulo*) predation rates on livestock [59], nest predation decreases when corvids are conditioned with visual stimuli following illness [60], and unpleasant odours reduce herbivory by pest mammals [27]. Habituation, particularly by intelligent mammals [21,22], can quickly diminish the effectiveness of deflective stimuli and the individual characteristics of a pest can influence the rate of habituation [61]. Rogue individuals can be attracted to stimuli that effectively deter most of the target pests, as, for example, polar bears (*Ursus maritimus*) responding to aggressive conspecific vocalizations [59]. Mixed evidence for the effectiveness of sensory stimuli in reducing human–wildlife conflict [42–44,62] may relate to a failure to consider these individual differences. Managers can apply cues intermittently, change the type and location of cues, use multiple cues simultaneously, and interrupt pests early during an animal's approach to minimize habituation. Live deterrents, such as guard animals (e.g., dogs, *Canis lupus familiaris*; llamas, *Lama glama*; and falcons, *Falco novaeseelandiae*), are ideal because they emit a full suite of sensory cues and can deliver negative reinforcement. These measures will work best when the attractant value of the resource is relatively low (low *VA*) compared to alternatives (high *MOC*). Increasing the perception of missed opportunity costs can be achieved by luring animals to more attractive cues (outlined earlier) in areas immediately adjacent to the resources we wish to protect. These 'push–pull' strategies that combine repellents and attractants have been applied successfully for insect control [63], but their utility for vertebrate control has not been adequately explored. Similarly, strategies that enhance Allee effects [64], analogous to the application of prey cues for chemical camouflage, could be particularly valuable when managing invasive vertebrate pests.

It is not always clear to managers whether rogues or recalcitrants are the main problem, or which motivations dominate the behaviour of target animals. Managers should work towards understanding the behavioural tendencies of problematic individuals, decide whether an attraction or deflection strategy best suits their situation, and then consider the appropriate suite of cues. Sensory cue strategies should then be trialled within existing management programs to determine where improvements can be achieved. Individual variability will alter the efficacy of any strategy; minimising the perceived danger of devices and altering missed opportunity costs will help to target the full range of behavioural variation. While applying a range of stimuli, managers must be mindful of unintended consequences for non-target species, such as negative sub-lethal effects of predator cues on the prey species they wish to protect [65]. Overall, the key in many cases will be to use an adaptive management strategy that provides a range of appropriate motivators targeting the spectrum of behavioural responses within the focal pest population(s) (e.g., Table 1).

Table 1. Examples of Stimuli Deployed to Attract or Deter Vertebrates[a]

| | Sensory Cue | 4F Motivational Stimuli: Food | Fornication | Fight | Fear |
|---|---|---|---|---|---|
| ATTRACT | Visual | Toy mouse [34] | Conspecific decoy [72] | Conspecific decoy [72] | Predator decoy [73] |
| ATTRACT | Olfactory | Bird odour [15] Fish oil [28] | Conspecific pheromone [15] | Conspecific scent glands [74] | Predator kairomones [29, 75] |
| ATTRACT | Auditory | Prey distress call [27] | Conspecific contact call [72] | Conspecific vocalisation [27] | Predator vocalisation [27] |
| ATTRACT | All three | Live prey [76] | Live conspecific [77] | Live conspecific "call-bird" [78] | Live predator [78] |
| DETER | Visual | Fladry (canids) [35] | Dead conspecific [79] | Conspecific model [80] | Predator decoy [68] |
| DETER | Olfactory | Herbivore repellent [61] | Sick conspecific odour [81] | Conspecific scent mark [82] | Predator odour (shark) [72] |
| DETER | Auditory | Biosonic repellent [64] | Conspecific distress call [44] | Aggressive conspecific call [64] | Predator vocalisation [19] |
| DETER | All three | NA | NA | NA | Live predator (livestock guard dog) [49] |

[a]Sensory cues are based on three primary senses (visual, olfactory, or auditory), or live animals, representing a combination of these senses. Stimuli are based on the 4F motivations of animal behaviour: food (energy demands), fornication (mating and other social interactions), fight (competition), and fear (predator avoidance). Individual variability will influence behavioural responses; for example, a stimulus that deters most individuals may attract others (e.g., aggressive conspecific vocalisation) or the rate of habituation can relate to an animal's personality [25,71-81].

## Concluding Remarks

Conventional pest management treats the population as homogeneous 'average' individuals. The mechanistic approach to managing pests outlined here provides additional strategies by tailoring sensory cues to the range of individual behavioural types. Greater focus on individual behavioural variability will help improve population-level outcomes and reduce the impacts of problematic individuals. While our framework provides a roadmap, numerous questions remain (see Outstanding Questions). Management that incorporates principles of behavioural ecology should test the ability of these ideas to increase effectiveness of interventions while leveraging opportunities to test behavioural theory in a natural context.

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## Outstanding Questions

How do we determine the proportion of difficult-to-manage individuals in a population? What factors explain variation among populations in the proportion of rogues or recalcitrants?

What factors affect the relative effectiveness, ease or cost of manipulating value (attractiveness), perceived risk, or missed opportunity costs as tools for pest management?

How do key motivators (4Fs; feeding, fleeing, fighting, fornication) vary across populations and individuals?

How do multimodal cues enhance or reduce overall effectiveness? Should all attractants or repellents be deployed simultaneously or cycled?

What roles do social cues play in facilitating learning and creating rogues or recalcitrants?

Do repellents simply displace the problem?

How long do learned experiences last (i.e., memory)? Can they be reset?

How can we strategically manage the challenges and opportunities of habituation to devices?

To what extent do individuals generalize their perception of risk based on signal detection? How can this be used to increase management effectiveness?

Can individual heterogeneity be effectively incorporated into ecological models (e.g., harvesting or population control models) to improve management predictions?

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